

THE DIET OF STELLER'S EIDERS WINTERING IN VARANGERFJORD, NORTHERN NORWAY

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ABSTRACT.—We examined the winter diet of Steller's Eiders (*Polysticta stelleri*) in Varangerfjord, northern Norway, by analyzing the esophagus content of 29 individuals (12 juveniles and 17 adults). A total of 8389 prey items of 31 species were identified: 13 species of gastropods (making up 68.4% of total number of items); 4 species of bivalves (18.5%); 12 species of crustaceans (13%); and 2 species of echinoderms (<0.1%). In terms of percentage aggregate wet weight 31.4% was gastropods, 22.6% was bivalves, and 41.4% was crustaceans. Juvenile eiders ate more crustaceans (\bar{x} = 61% aggregate w.w.) than adults (\bar{x} = 26%, $P < 0.05$), possibly because they were in poor body condition and may have had higher energy requirements than adults. Adults tended to eat more gastropods (\bar{x} = 41% vs 22%) and *Mytilus edulis* (\bar{x} = 27% vs 12%) than juveniles. There were only small differences between sexes. Most of the prey items were of species known to be associated with kelp plants, especially *Laminaria hyperborea*, suggesting that Steller's Eiders obtain a large proportion of their prey directly from the vegetation. Received 16 April 1999, accepted 19 Oct. 1999.

The winter diets of most sea ducks (tribe Mergini and Somaterini) are well known, but not for the Steller's Eider (*Polysticta stelleri*). This species inhabits remote areas, breeding along the Arctic coasts of Siberia and Alaska and wintering in sub-arctic waters in Alaska, East-Asia, and northwestern Europe. About 15–25% (30,000–50,000 birds) of the world population winters in northwestern Europe, most (> 80%) in Varangerfjord in northeastern Norway and along the coast of the Kola Peninsula in northwestern Russia (Nygård et al. 1995). North American researchers that have quantified the diet of the Steller's Eider during the breeding season (Cottam 1939), molt (Petersen 1980, 1981), and winter (Metzner 1993) have found that it consists mostly of small gastropods, bivalves, and crustaceans. In northwestern Europe the diet of the species is poorly known (Siivonen 1941, Mitchell et al. 1996). Here we present quantitative information on the diet of the population wintering in Varangerfjord.

METHODS

Study area.—The study area was on the northern side of Varangerfjord (Fig. 1). The area consists of

shoreline dominated by gently shelving coastal profiles with shallow water (<50 m) that may extend several km out from the shore (Fox and Mitchell 1997). The benthic communities in this area are dominated by large beds of kelp, especially *Laminaria hyperborea* (Bustnes and Systad, unpubl. data). Flocks consisting of both juvenile and adult eiders, of both sexes fed by diving in shallow waters (< 5 m; Bustnes and Systad, unpubl. data). Steller's Eiders were collected during winter (late November to early April) in the area between Ekkerøy (70° 04' N, 30° 05' E) and Urdnes (70° 08' N, 30° 15' E; Fig. 1), from November 1996 until April 1998. Birds were shot during daylight hours using a shotgun from a small boat, or with a .22 caliber rifle from the shore.

All birds were aged and sexed using plumage characteristics (Palmer 1976) and the presence or absence of a bursa of Fabricius. They were either dissected on the same day that they were shot or frozen shortly after they had been killed. The esophagus (including the proventriculus) and gizzard were removed and their contents kept separate and frozen immediately after dissection. For the analyses, food items from the esophagus and proventriculus were combined, but kept separate from the gizzard contents. We excluded the gizzard from the analyses because its contents were fragmentary. The food items were identified to species whenever possible. The prey items were counted and weighed on a Precisa 100A-300M balance to the closest 0.001 g. Each species was weighed separately except for the crustaceans which were separated into amphipods and isopods. Some esophagi contained damaged crustaceans from which species or number of separate individuals could not be determined. This damaged matter was only used in the proportion aggregate wet weight of the total of crustaceans and not included in the total number of prey items.

Data were summarized as the proportion of the food total for all individuals (frequency of occurrence and wet weight) and the mean frequency and the mean

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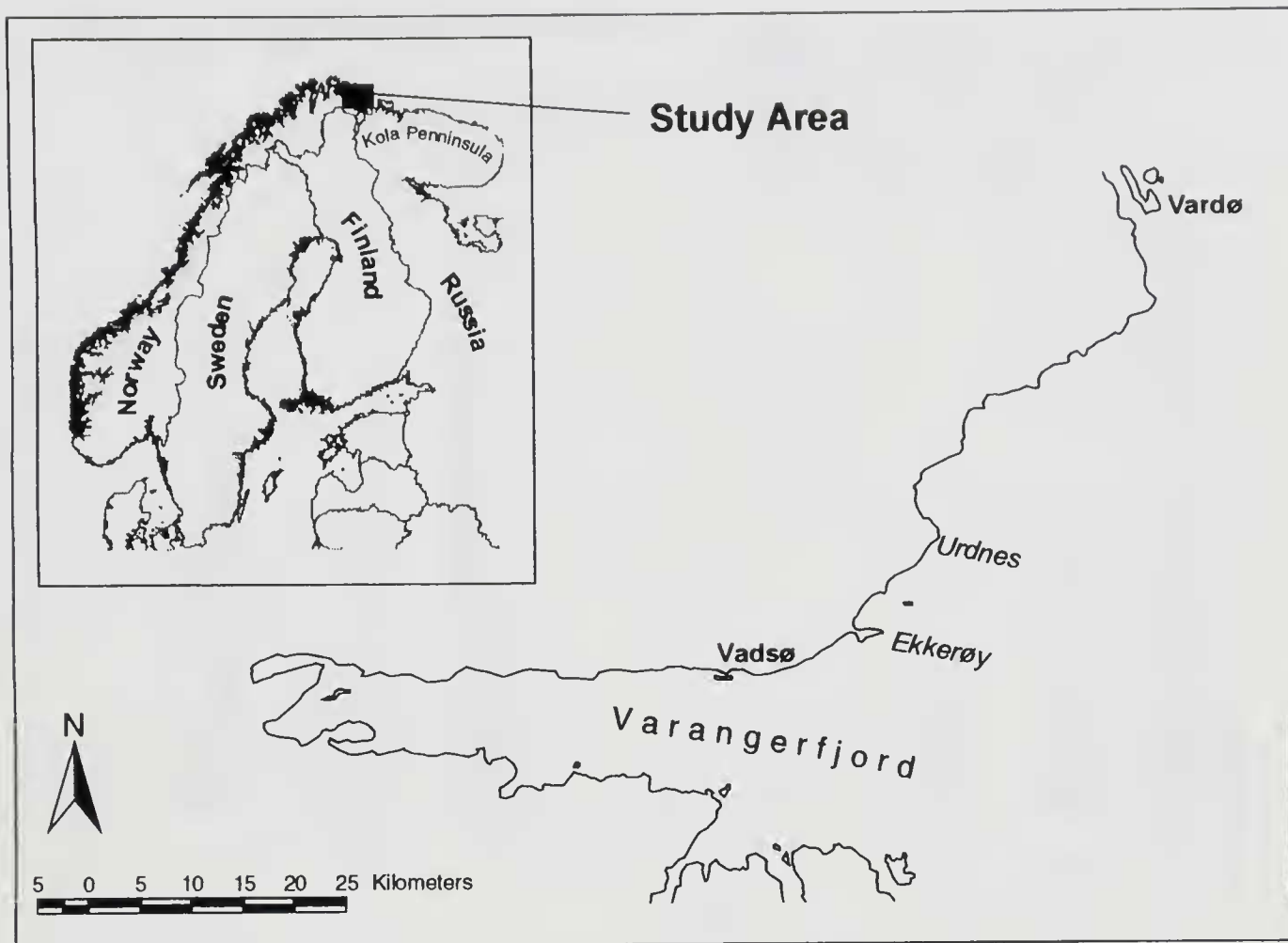


FIG. 1.—The study area in Varangerfjord, northern Norway.

aggregate percent wet weight among individuals (Table 1, see Krapu and Reinecke 1992 for a review).

Analyses.—We analyzed the proportions of aggregate wet weight using two-way ANOVAs (SAS, version 6.04 on an IBM PC; PROC GLM, SAS 1990). Because of lack of normality (tested by PROC UNIVARIATE) we used rank transformation (PROC RANK, SAS 1990; Conover and Iman 1981, Potvin and Roff 1993). Gastropods and crustaceans were pooled into groups and no species was analyzed individually. Among bivalves, only *Mytilus edulis* was a common prey of a large number of birds and was the only species we analyzed statistically. The dependent variable was the proportion of each prey type (wet weight of the prey type in question divided by the weight of the total prey content of each bird). Independent variables were sex and age of the bird. All models were tested for interactions, which were removed when not significant. Standard errors (SE) are given for all means. The sample consisted of 29 birds, 12 juveniles (6 males and 6 females) and 17 adults (11 males and 6 females).

RESULTS

Thirty-one prey species were found: 13 species of gastropods, 4 bivalves, 12 crustaceans, and 2 echinoderms (Table 1). Some birds also

contained remains of polychaets. A total of 8389 prey items were identified, of which 68.4% were gastropods, 18.5% were bivalves, and 13% were crustaceans (Table 1). In terms of aggregate wet weight, 31.4% was gastropods, 30.6% was bivalves and 38% was crustaceans (Table 1). The differences between frequency and weight proportions were due to large numbers of small gastropods (Fig. 2).

Gastropods.—Gastropods were found in 97% of the birds. *Margarites helicius* and *Skeneopsis planorbis* made up 18.9% and 53.6%, respectively, of the total gastropod numbers (Table 1). However, 99.1% ($n = 3047$) of the *S. planorbis* were found in adult male eiders, one bird contained 2700 individuals (87.8%). The mean percentage by weight of gastropods in adults was 40.5 ± 8.1 (SE)%, while for juveniles it was $21.6 \pm 8.3\%$ (Fig. 2). *Margarites helicius* and *Lacuna vineta* made up the largest proportions of the diet by mass in both juveniles ($3.6 \pm 1.1\%$ and $12.2 \pm 8.2\%$, respectively) and adults ($15.6 \pm 6.0\%$ and $12.7 \pm 4.0\%$, respectively). There

TABLE 1. Esophageal content of 29 Steller's Eiders collected in Varangerfjord, northern Norway, November 1996 to April 1997.

Taxa	No. of specimens (%)	Mean \pm SE frequency	% of total wet weight	Mean \pm SE wet weight	No. of birds (%)
Gastropoda					
<i>Littorina saxatilis</i>	30 (0.36)	1.30 \pm 0.88	0.93	2.39 \pm 2.34	5 (17.24)
<i>L. obtusata</i>	139 (1.66)	0.61 \pm 0.26	2.03	1.14 \pm 0.76	8 (27.59)
<i>Thais lapillus</i>	2 (0.02)	0.19 \pm 0.19	0.05	0.03 \pm 0.03	1 (3.45)
<i>Trophonopsis truncatus</i>	3 (0.04)	0.25 \pm 0.22	0.13	0.26 \pm 0.22	3 (10.35)
<i>Lacuna vincta</i> ^a	667 (7.95)	11.87 \pm 2.80	10.19	12.48 \pm 4.03	20 (68.97)
<i>L. neritodea</i> ^a	136 (1.62)	1.02 \pm 0.62	1.44	0.94 \pm 0.76	6 (20.69)
<i>Margarites helicinus</i> ^a	1087 (12.96)	18.33 \pm 4.24	11.37	10.65 \pm 3.65	23 (79.31)
<i>M. groenlandicus</i> ^a	28 (0.33)	1.11 \pm 0.75	1.12	1.90 \pm 1.19	8 (27.59)
<i>Rissoa</i> spp. ^a	184 (2.19)	2.53 \pm 0.75	0.61	0.42 \pm 0.13	15 (51.72)
<i>Ouoba</i> spp. ^a	355 (4.23)	2.22 \pm 1.05	0.31	0.18 \pm 0.07	10 (34.48)
<i>Buccinum groenlandicum</i>	3 (0.04)	0.07 \pm 0.06	0.03	0.02 \pm 0.01	2 (6.90)
<i>Skeneopsis planorbis</i> ^a	3074 (36.64)	5.51 \pm 2.86	2.69	1.59 \pm 1.42	12 (41.38)
<i>Amacea testidunalis</i>	11 (0.13)	0.22 \pm 0.12	0.32	0.39 \pm 0.21	5 (17.24)
Unidentified species	20 (0.24)	0.28 \pm 0.16	0.24	0.27 \pm 0.20	6 (20.69)
Total of Gastropoda	5739 (68.41)	45.53 \pm 5.67	31.44	32.67 \pm 6.02	28 (96.55)
Bivalvia					
<i>Mytilus edulis</i> ^a	750 (8.94)	13.86 \pm 4.10	27.02	21.00 \pm 5.91	20 (68.96)
<i>Tutoria minuta</i> ^a	782 (9.32)	2.17 \pm 1.07	1.26	0.64 \pm 0.46	12 (41.38)
<i>Musculus discors</i>	10 (0.12)	0.05 \pm 0.02	0.28	0.13 \pm 0.12	5 (17.24)
<i>Hiatella arctica</i>	1 (0.01)	0.01 \pm 0.01	—	—	1 (3.45)
Unidentified species	11 (0.13)	0.08 \pm 0.04	2.02	0.81 \pm 0.44	5 (15.63)
Total of Bivalva	1554 (18.52)	16.16 \pm 4.26	30.59	22.58 \pm 6.03	25 (86.20)
Polyplacophora spp.	1 (0.01)	—	—	—	1 (3.45)
Crustacea					
Isopoda					
<i>Jaera</i> spp.	51 (0.61)	1.84 \pm 1.83	—	—	2 (6.90)
<i>Idotea pelagica</i> ^a	3 (0.04)	0.13 \pm 0.13	—	—	1 (3.45)
<i>I. emarginata</i> ^a	169 (2.01)	5.61 \pm 3.86	—	—	3 (10.35)
<i>I. granulosa</i> ^a	100 (1.19)	3.44 \pm 2.80	—	—	8 (25.00)
<i>I. baltica</i> ^a	11 (0.13)	0.12 \pm 0.12	—	—	2 (6.90)
Unidentified species	54 (0.64)	2.03 \pm 1.16	—	—	4 (13.79)
Total of Isopoda	388 (4.63)	13.19 \pm 5.55	14.42	14.50 \pm 5.40	12 (41.38)
Amphipoda					
<i>Gammarus oceanicus</i>	212 (2.53)	13.10 \pm 4.94	—	—	13 (44.83)
<i>Gammarus homari</i>	5 (0.06)	0.18 \pm 0.11	—	—	5 (17.24)
<i>Amphithoe rubricata</i> ^a	327 (3.90)	5.04 \pm 1.87	—	—	12 (41.38)
<i>Auonyx sarsi</i>	8 (0.10)	0.21 \pm 0.12	—	—	4 (13.79)
<i>Calliopius laeviusculus</i> ^a	14 (0.17)	0.56 \pm 0.37	—	—	4 (13.79)
<i>Onisimus edwardsi</i>	1 (0.01)	0.03 \pm 0.03	—	—	1 (3.45)
<i>Caprella</i> spp. ^a	67 (0.80)	3.31 \pm 2.75	—	—	6 (20.69)
Unidentified species	70 (0.84)	1.30 \pm 0.77	—	—	6 (20.69)
Total of Amphipods	704 (8.39)	24.40 \pm 5.42	14.53	18.64 \pm 5.76	23 (79.31)
Total of Crustacea	1092 (13.01)	37.59 \pm 6.56	37.97	41.46 \pm 7.38	24 (82.75)
Polychaeta	—	—	—	—	3 (10.34)
Echinodermata					
<i>Stronglyocentrotus droebachiensis</i>	1 (0.01)	—	—	—	1 (3.45)
<i>Ophiopholis aculata</i>	1 (0.01)	—	—	—	1 (3.45)

^a Species commonly found on kelp plants (After Christie 1995, Norderhaug 1998).

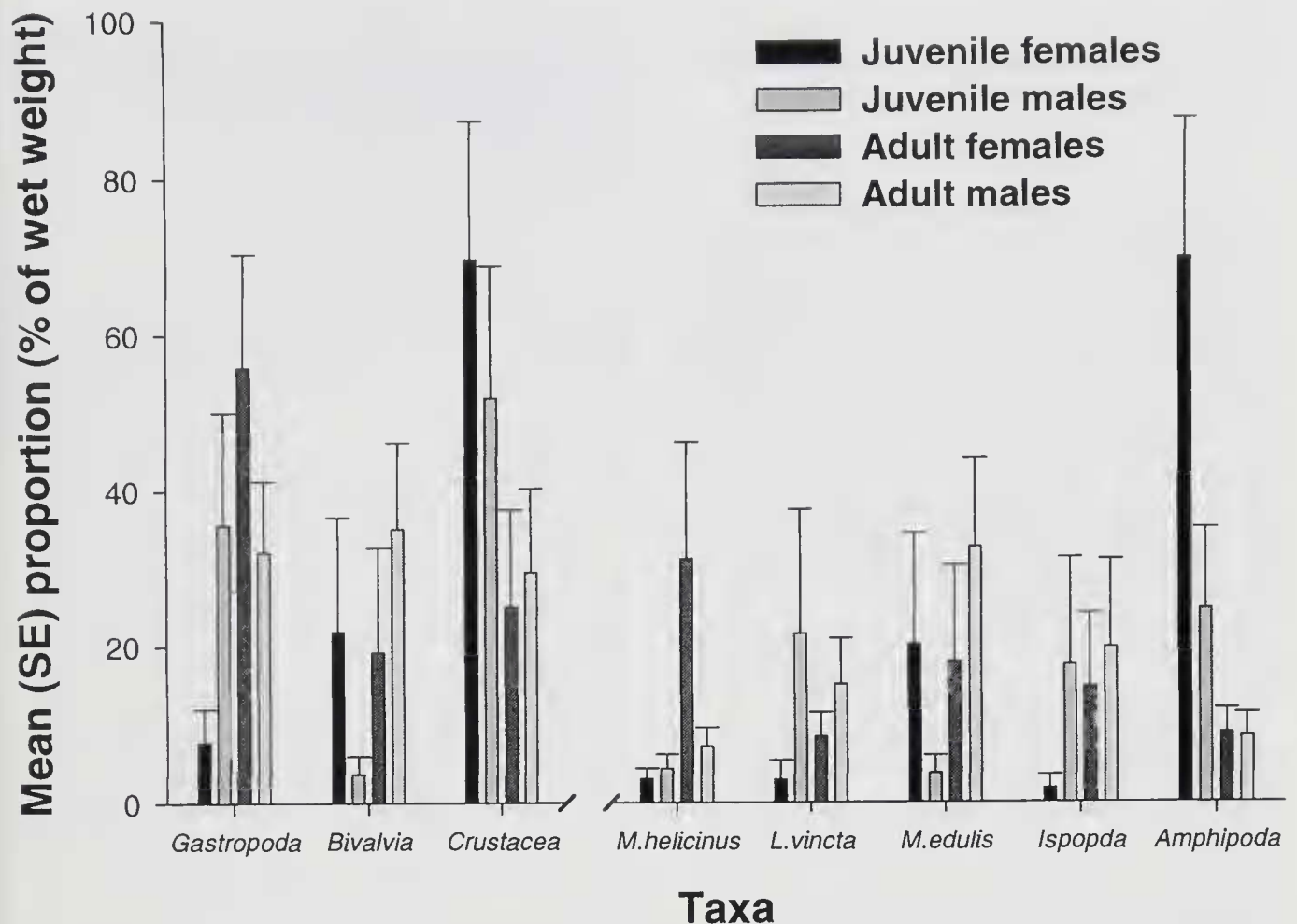


FIG. 2. The proportion (mean \pm SE) of various prey types of Steller's Eiders, collected in Varangerfjord, northern Norway, November 1996 to April 1998.

was a significant interaction in the model between age and sex for proportion of aggregate wet weight consisting of gastropods ($F_{1,25} = 5.03$, $P < 0.05$), consequently we analyzed the sexes separately. Adult females ate significantly more snails than did juvenile females ($F_{1,11} = 10.01$, $P = 0.01$) but no such differences were found among adult and juvenile males ($F_{1,17} = 0.05$, $P > 0.05$; Fig. 2).

Bivalves.—Eighty-six percent of the birds had eaten bivalves, and 1554 specimens were identified (Table 1). Of these 48.3% were *Mytilus edulis* and 50.3% were *Turtonia minuta*. However, 99% of the *T. minuta* were found in adult male eiders; two males contained 98.5% of the total. Bivalves made up 30.6% of the aggregate wet weight (Table 1), of which 88.3% was *M. edulis*. In adult eiders, bivalves made up $29.5 \pm 8.6\%$, but in juveniles they made up $12.8 \pm 7.6\%$. The mean weight proportion of *M. edulis* was $27.4 \pm 8.5\%$ in adults and $11.9 \pm 7.3\%$ in juveniles (Fig. 2). Neither sex ($F_{1,26} = 0.08$, $P > 0.05$) nor age

($F_{1,25} = 1.66$, $P > 0.05$) had significant effects on the aggregate weight proportions of *M. edulis* in the diet (Fig. 2).

Crustaceans.—Overall, 83% of the birds were found to have eaten crustaceans. Of 1092 crustaceans identified, 64.5% were amphipods and 35.5% were isopods (Table 1). The most numerous amphipods were *Gammarus oceanicus* (30.1%) and *Amphithoe rubricata* (46.5%), while *Idotea emarginata* (43.6%) and *I. granulosa* (25.8%) were the most common isopods (Table 1). Overall 38% of the aggregate weight consisted of crustaceans (Table 1), of which isopods made up 49.8% and amphipods 50.2%. The mean proportion of crustaceans in juveniles was $60.7 \pm 12.0\%$ including those not identified beyond the crustacean group. When excluding the unidentified group, $9.6 \pm 7.0\%$ were isopods and $33.0 \pm 8.6\%$ were amphipods. The proportion of crustaceans in adults was $27.9 \pm 8.1\%$ ($18.0 \pm 7.8\%$ isopods and $8.5 \pm 2.6\%$ amphipods; Fig. 2). Age ($F_{1,26} = 5.5$, $P =$

0.027), but not sex ($F_{1,26} = 0.50$, $P > 0.05$) had a significant effect on the proportion aggregate wet weight of crustaceans.

DISCUSSION

In terms of biomass, gastropods, bivalves, and crustaceans made up nearly equal proportions (30–40%) of the Steller's Eider winter diet. The prey species that were of particular importance (Table 1) are all common species in hard bottom communities, especially kelp beds, along the Norwegian coast (Christie 1995, Skadsheim and Rinde 1995, Norderhaug 1998). Metzner (1993) studied wintering Steller's Eiders in Izembek Lagoon in Alaska and found that 15% of the diet consisted of gastropods, 29% bivalves, and 30% crustaceans, indicating a similar diet as the Steller's Eiders in Varangerfjord. Petersen (1980, 1981) showed that *M. edulis* and the amphipod *Anisogammarus pugettensis* made up the majority (about 40% each) of the diet of molting Steller's Eiders in Nelson Lagoon, Alaska. In our study *M. edulis* was the species of which the birds ate the largest biomass (27%), probably a result of the ubiquitous nature of *M. edulis* (Seed 1976) and its availability in the study area. Steller's Eiders appear to have a higher proportion of amphipods and isopods in their diet than most other sea ducks (Cottam 1939; Madsen 1954; Johnsgaard 1975; Palmer 1976; Petersen 1980, 1981; Metzner 1993). This suggests that the Steller's Eider specializes in catching mobile prey. Moreover, because crustaceans have a much larger energy density per gram than shelled prey (Goudie and Ankney 1986, Guillemette et al. 1992), the high proportion of crustaceans eaten by Steller's Eiders suggests that the species has high energetic requirements. Larger sea ducks such as other eiders (*Somateria* spp.) and scoters (*Melanitta* spp.) usually feed on larger prey with lower energy content, mainly bivalves and echinoderms (Cottam 1939; Madsen 1954; Palmer 1976; Goudie and Ankney 1986; Bustnes and Erikstad 1988, 1990; Guillemette et al. 1992). The only other small-bodied sea ducks in northern Norway, the Oldsquaw (*Clangula hyemalis*), may also eat large proportions of isopods and amphipods. Generally they have a more diverse diet, including fish and fish roe, than the Steller's Eider (Cottam 1939; Madsen 1954; Sanger and

Jones 1984; Johnson 1984; Goudie and Ankney 1986; Bustnes and Systad, unpubl. data).

The reason juveniles ate more crustaceans than adults (means of 60% vs 25%), might be that the former were in poorer body condition (Bustnes and Systad, unpubl. data) and needed more energy to survive. Foraging where the risk of starvation is minimized is often referred to as 'risk prone' foraging (Krebs and Kaclenik 1991) and may increase the survival probability if the expected energy budget is negative. Mean intake rate from a predictable food source may not result in a positive energy budget, but high returns from a variable source might. If the expected energy budget is positive, animals may benefit from selecting the least variable food source and be 'risk averse' (see Krebs and Kaclenik 1991 for a review). While mollusks and bivalves are more or less stationary, crustaceans are mobile, probably making them less predictable prey. Birds in good condition may feed safely on predictable food sources with lower energy content, while birds in poor condition, such as juveniles, may need food with high energy density to survive (Guillemette et al. 1992).

In Varangerfjord the Steller's Eiders predominantly feed in areas with underwater vegetation, especially in kelp forest dominated by *Laminaria hyperborea* (Bustnes and Systad, unpubl. data). Such kelp beds are known to have a high diversity and biomass of potential prey for sea ducks. Recent studies have documented the distribution of invertebrates on the kelp plants along the Norwegian coast (Christie 1995, Skadheim and Rinde 1995, Norderhaug 1998). By comparing the species assemblages in kelp forest to the diet of Steller's Eider in Varangerfjord we found that more than 90% of the prey items were of species that commonly inhabit kelp plants (Table 1; Christie 1995, Norderhaug 1998). This strongly suggests that the vegetation itself is an important feeding habitat for this species. A similar conclusion may be drawn from a study in Izembek Lagoon, Alaska (Metzner 1993) where Steller's Eiders predominantly fed among eel grass (*Zostera marina*).

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